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NOTES AND LITERATURE

FAUNAL DISPERSAL[1]

THE widely different conclusions drawn by different students from the same facts is well illustrated by Matthew's recent paper on the geographic distribution of animals.[2] Although these differences are of many and varied sorts a fundamental one seems to be concerned with the question as to whether the peripheral part or the central part of the range of a group contains the more progressive members of that group.

The idea which is held, either consciously or unconsciously, by many is that after a group has arisen it spreads; and the migrants, meeting new conditions, develop new characters. These new forms then spread still further and develop other characters. Thus the more primitive members remain at or near the point of origin of the group; the successively more progressive members will be found at respectively greater distances from this point. According to this theory we may trace *backward* the dispersal of the group by following the distributions of the several members from the most progressive to the most primitive. We may not be able to follow this line to the actual point of origin of the group for the most primitive members may not be alive now and we may be unable to find their fossil remains. However, as organisms usually extend their range in more than one direction, we may be able to trace several lines of dispersal and deduce that the point of origin was near the place at which these lines tend to converge.

The other theory is as nearly the opposite as can be. According to it the first progressive makes its appearance well within the range of the primitive members of the group. If the new form is not an improvement over the primitive one, it dies out. If it be an improvement, it crowds the primitive form which is forced to leave its place of origin and migrate. It is sometimes made a part of this theory (but it is not a necessary part) that the reason a new form appeared among the old was that the new climatic conditions appeared there and that if the old form could, in its migration, keep in climatic conditions suited to it, well and good; if it could not, it either died out or became adapted to the climatic conditions into which it was forced without, however, losing all the earmarks of its primitiveness. Later still, newer forms appeared at the old stand and forced their predecessors still further away. Therefore, if we follow the distribution of the several members of the group from the most progressive to the most primitive, we will trace the dispersal of the group *forward,* not backward.

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[1] Read at the February 15, 1916, meeting of the N. Y. Entomological Society.

[2] W. D. Matthew, 1915, "Climate and Evolution," *Annals*, N. Y. Acad. of Sciences, XXIV, pp. 171–318.

It would probably be impossible to decide, either by logomachic methods or by watching present-day movements of species, which of these two theories is correct. However, we are not left without hope because paleontologists are daily digging up evidence which, when sufficiently complete and properly translated, will leave us in no doubt as to the history of the dispersal of certain groups, and there is little doubt that the same general principles which hold for those groups will apply to others concerning which we have not and probably never will have fossil record. Of course details may differ from group to group, but it is not probable that there is one set of laws for mammals and another for reptiles, one for birds and another for insects, that nature constructed a trans-oceanic bridge for one group, but stationed a guardian angel on it to prevent the passage of others. The chief differences probably were such as the differing responses of the different groups to changes of the environment and the differing powers of different groups in overcoming given barriers to dispersal.

Next to that brought about by the holding of the diametrically opposing theories just discussed, perhaps the most important source of confusion is in not keeping clearly distinct "center of origin," "center of dispersal" and "center of greatest development." They may all be in the same region or they may be as far removed from each other as the earth's surface will permit but they are not the same. A group may arise at *A* and move to *B,* from which point there are easy paths of migration to *C, D, E* and *F.* It may, and doubtless would, go to all of these but it might find that *E* alone furnishes good conditions for its future development. Its center of origin would then be at *A,* its center of dispersal would be at *B,* and its center of greatest development at *E.* According to the first theory discussed above, the more primitive forms would be found at *A* or *B* and the later developments at *C, D, E* and *F,* but chiefly at *E.* According to the second theory, *C, D, E* and *F* would have the primitive forms (although they might be much modified, especially at *E*) and the progressive members of the group would be at *A* or *B.*

Adams[3] did good service in bringing together a number of suggested "criteria for the determination of centers of dispersal." It was not to be expected, and doubtless Adams did not expect, that all of them would stand up under a test. Without attempting to exhaust the subject, present anything new or review all that has been said about them, certain notes may be made in connection with this discussion, taking up the criteria *seriatim.*

1. *Location of the Greatest Differentiation of the Type.*—I believe it is more than a mere question of definition to say that the offering of this criterion is an instance of the confusion of "center of dispersal" with "center of greatest development." Two of the stock illustrations of great differentiation are those of marsupials in Australia and lemurs in Madagascar. Since these groups are so greatly developed on the respective islands they should, according to this criterion, have spread out from these islands to the rest of the world. Unless the paleontological evidence, as brought together and interpreted by Matthew, is false, that was not the history of these cases. On the other hand, wherever their points of origin were, their ancestors got into the Holarctic region and then spread in various directions. Now, if this be true, their center of dispersal would be Holarctica, although their greatest differentiation *at the present time* is toward the other end of the world. Lest the quibble should be raised by others, it should be stated that the real fundamental center of dispersal of a group is its center of origin and that there are

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[3] C. C. Adams, 1902, "Southeastern United States as a Center of Distribution of Flora and Fauna," *Biol. Bull.*, VII, p. 122. After the present paper had gone to the press I obtained through the kindness of Professor Adams, a portion of "An Ecological Survey of Isle Royale, Lake Superior" prepared under his direction and published (1909) as a part of the Report of [Michigan] Board of the Geological Survey for 1908. In this he takes up, again, these criteria. He says "It should be clearly emphasized that it is the convergence of evidence from many criteria which must be the final test in the determination of origins rather than the dependence upon any supposedly absolute criterion." He discusses the various criteria in greater detail than was done in his 1902 paper and adds, as another criterion, "Direction indicated by seasonal appearance; vernal suggesting boreal or montane origin and aestival as austral or lowland derivation." I regret that I did not have earlier access to this paper but as I did not base my present remarks on his 1902 contribution with the idea of criticizing it in particular but for the purpose of pointing out the danger of relying too confidently on such evidence, it is probably unnecessary to change the text of this article in order to meet the expanded discussion in the 1909 paper by Adams. This is especially true since I intentionally omitted, for the sake of brevity, reference to certain papers, such as the one by Tower (1906), which bear on the same subject.

other centers of dispersal wherever there are branches in the forward movement of the group; but I understand the usual meaning of "center of dispersal" to be the point or points from which the principal lines went out which resulted in the wide spread of the group.

2. *Location of Dominance or Great Abundance of Individuals.*—This criterion seems futile. A group may have moved in all directions from a given region and died out entirely in the region from which it moved. Nothing is more clearly established than the changeableness of geologic climate and hence of all environmental factors and we know of many instances where nothing is left of a group of organisms but fossil remains in the regions of their former abundance and a few living remnants in far-away, protected spots. If, as seems very clear, we can not believe that even the most populous of these havens marks the center of dispersal of such a group, neither can we apply this criterion with safety to any other group. The area of present dominance is merely that area, of all those now inhabited by a group, which is at the present time most suited to the group—unless, of course, it has arrived in a more suitable area so recently that it has not had time to develop its dominance.

3. *Location of Synthetic or Closely Related Forms.*—This criterion will be considered more in detail later, but it may be remarked in passing that the location of closely related forms is of little help in arriving at the center of dispersal unless we know whether these forms are more primitive or the reverse and unless, furthermore, we have selected the right one of the two opposing theories which were mentioned in the beginning of this discussion.

4. *Location of Maximum Size of Individuals.*—It is difficult to see why individuals should be larger at the center of dispersal than elsewhere. Possibly they may be larger the nearer they are to present-day, optimum environmental conditions, but this is probably not often, and certainly not necessarily, anywhere near the ancient center of dispersal.

5. *Location of Greatest Productiveness and its Relative Stability, in Crops.*—Adam says this criterion is very closely related to the second one. If so, it fails for the same reason. Also, it would seem that the latter part of this criterion conflicts with criterion number one—"greatest differentiation of type."

6. *Continuity and Convergence of Lines of Dispersal.*—This certainly ought to work, provided we follow the lines in the right direction. The difficulty is that north and south lines on a more

or less spherical world converge either way we go. Furthermore, if we place confidence in oceanic bridges which have been washed away, piers and all, the lines of dispersal are apt to be frequently discontinuous.

7. *Location of Least Dependence upon a Restricted Habitat.*—For example, certain plants and animals which, in the region of New York City, are found only in sphagnum bogs, such as those of the Jersey pine barrens, occur more widely distributed farther north. According to this criterion their center of dispersal would be in the north and this may be true. Again, lizards occur, in the region of New York City, only or chiefly in these same pine barrens, while farther south they run about wherever they can get sunshine. According to this criterion the ancient center of dispersal of lizards was somewhere near the equator, but this may not be true.

8. *Continuity and Directness of Individual Variations or Modifications Radiating from the Center of Origin along the Highways of Dispersal.*—This criterion is probably stated rather more fully than was meant. If we knew all this, the problem would be solved. Perhaps Adams meant that continuity and directness of modifications (''individual variations'' gets us into the biometric-mutation discussion and that is another story) point out the highways of dispersal from the point of origin. His reference on the next page to Osborn's law of adaptive radiation indicates that this is the proper interpretation of this criterion and, if so, the present author has no quarrel with it except to point out once more that we are left in doubt as to which way to follow the lines.

9. *Direction indicated by Biogeographical Affinities.*—I am not certain as to what this means. I suppose a given group which is neotropical at the present time has biogeographical affinities with other present-day neotropical groups. If we know the centers of dispersal of the other groups we have a working hypothesis concerning the center of dispersal of the group in question. If this be what is meant, it seems to be probable.

10. *Direction indicated by the Annual Migration Routes, in Birds.*—This criterion is meant to apply only to birds and I fear we know too little concerning the intricate problems of bird migration to say whether their present-day routes of annual migration follow the route of ancestral dispersal or not. Probably they do not, as the birds would be expected to change their routes with changing environmental conditions. Furthermore, although it is believed that birds return to their ancestral home

to breed, this is not so firmly established as to leave no doubt about which is going and which is coming.

Adams clearly stated that these criteria are for use where "we do not have paleontological evidence in sufficient abundance to materially aid us," but I confess to a feeling that we must still depend on paleontology to give us the general laws of dispersal. It is for this reason that such papers as Matthew's seem to me so helpful. I regret that the organisms in which I am most interested did not leave more marks on the sands of time, but if the great majority of mammalian groups left records to show that they followed a certain set of lines of dispersal and the end result is of a given character, it seems worth while to compare the end results of the dispersal of other forms with those of the mammalian groups. If the comparison is close, the deduction that the lines of dispersal also are comparable seems not unsafe. It certainly seems unwise to construct trans-oceanic bridges where conservative geologists say there could have been none, especially if they must be made so tenuous that only insects, spiders, snails, earthworms, fresh-water fishes and such small fry can cross, mammals being forbidden.

Several of the criteria given by Adams which appear to fail in helping us discover the ancient centers of dispersal seem to be indicators of present or potential centers. Thus the first one: a region where there is a "great differentiation of type" within a group would seem to be a region prepared to send members of that group into all the world. If paths exist or chance intervenes, this group should be able to fit some, at least, of its many different types into the new environments which it encounters in its spread. If all the surrounding territory is already occupied by more successful competitors, that merely means that there are no paths for the dispersal of this group. One of the real, but sometimes overlooked, barriers to faunal spread is the presence of competitors. This, however, does not negate the idea that a region of "great differentiation of type" is a potential center of dispersal.

In somewhat the same way the region of "dominance or great abundance of individuals" is a potential center of dispersal. The case is not so clear; but it would seem that where there is a *relatively* large supply of individuals more could be spared for, or would be forced into, colonization efforts than where there are relatively few.

This suggests that what was the center of greatest development (especially in variety of types) became the center of dispersal, and that what is now the center of greatest development is or will be a new center of dispersal provided there are means of dispersal. There seems to be a genetic relationship between these three centers and, of course, at the beginning the center of origin is also the other two.

Little need be said here about means of dispersal except to point out what Matthew also emphasized, namely, that time is long and luck is real. Those of us who have been brought up on the doctrine of evolution by selection of "chance" variations should have a whole-hearted respect for that sometimes abused word. Those who believe there has been time enough for alert Nature to seize upon enough chances to differentiate 400,000 species of insects, for example, need not strain unduly in swallowing the notion that a very small proportion of these have been able to get across relatively short stretches of water without a bridge. Those who believe that Nature not only seized upon but made opportunities for the differentiation of species should have no trouble in discovering easier ways for her to help her creatures spread their range than by raising up long narrow portions of the ocean bed for a certain few to cross dry shod and then sinking it to the discomfiture of those which are not of the elect.

Insects probably get about as easily as any creatures because most insects fly or may be blown long distances and, furthermore, the majority have at least two distinct stages in their life cycle during which they remain inert and without the necessity of feeding. If mammals can reach islands not connected by bridges, surely insects of many kinds can. Matthew places great stress on natural rafts as a means of transporting mammalian fauna. After giving briefly a "series of facts and assumptions [which] may serve to give some idea of the degree of probability that attaches to the hypothesis of over-sea transportation to account for the population of oceanic islands" he says:

> If then we allow that ten such cases of natural rafts far out at sea have been reported, we may concede that 1,000 have probably occurred in three centuries and 30,000,000 during the Cenozoic. Of these rafts, only 3,000,000 will have had living mammals upon them, of these only 30,000 will have reached land, and in only 300 of these cases will the species have established a foothold.[4] This is quite sufficient to cover the dozen or two cases of mammalia on the larger oceanic islands.
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> Few of these assumptions can be statistically verified. Yet I think that, on the whole, they do not overstate the probabilities in each case.

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[4] Matthew apparently changed, between pages 206 and 207, his ideas concerning the probabilities. However, it is the general notion and not the actual figures which is important.

They are intended only as a rough index of the degree of probability that attaches to the method, and to show that the populating of the oceanic islands through over-sea transportation, especially upon natural rafts, is not an explanation to be set aside as too unlikely for consideration.

I confess to some haziness as to the probabilities here set forth, but, if they are anywhere near true, entomologists need not worry. In addition to their creatures not needing rafts as badly as do mammals, it is certainly probable that every, not "one in a hundred," natural raft big enough to be noticed and recorded by voyagers contained not one, but many, insects. Smaller rafts or even single trees might contain many individuals of several species and, since a single fertilized female gives birth to many offspring, the chance of a given species establishing itself on virgin soil is much greater than it is in the case of mammals. Furthermore, insects have been dispersing since before the Carboniferous. Many of the islands may not be that old, but this simply means that insects have had a chance at such an island since the first wavelets rippled about its uplifting peak. The one thing which may be comparatively disadvantageous to insects is that many of them are rather closely bound up in their food relations with certain plants, but this disadvantage is somewhat decreased by the fact that, if phytophagous insects are carried on natural rafts, their food plant is likely to be a part of the material which makes up the raft and both may be established together. The pros and cons are numerous and involved. It is a balancing of probabilities with the burden of proof on the side which claims the right to make over major features of the earth's surface in the face of contrary geological evidence.

If this be true for the scant fauna of oceanic islands, what shall we say of the suggested bridges, running this way and that, across the oceans for the purpose of connecting continental faunas and floras, especially in equatorial regions? Mercator gave us a map of the world so constructed that the longitudinal lines are parallel from the north pole to the south. Now the fact is that a degree of longitude equals approximately 111,300 meters at the equator, 104,600 meters at 20° latitude, 85,400 meters at 40°, 55,800 meters at 60°, 19,400 meters at 80°, and no meters at the poles. Therefore the equatorial distances on Mercator's projection are relatively far too short. On the globe or on a proportional projection in which a meter at the equator is as long as a meter in Alaska we see that north of the Tropic of Cancer in the eastern hemisphere lies a huge land mass consisting of Europe, northern Africa and most of Asia. This mass almost touches at its northeastern corner the somewhat smaller mass of North America. The intervening space, Bering Strait, is only about sixty-five miles wide, very shallow, and dotted with islands. The other gap between these masses is somewhat wider, but still not so great as the shortest distance between South America and Africa. Thus the arctic region is almost encircled by land and itself contains much land. The earth's surface is really one huge northern land mass with three southward projections, namely America, Africa and the East Indian Islands, including Australia. Antarctica is a small disconnected mass at the other end. A species or group of species originating in, or getting into, the far north could, as far as the present configuration of the continents goes, populate the earth and have solid ground under its feet most of the way.

Probably one of the main reasons for the little consideration which students of geographic distribution have given to this route of dispersal is the present climatic conditions in the far north. It seems to have been easier to imagine the ocean's bottom heaved up between Africa and South America than to conceive of a different climate in the northern regions. Yet we have definite and incontrovertible evidence of mild arctic climate in at least several geologic periods, while the only moderately strong evidence of a bridge across the Atlantic, for example, is the presence of related or identical forms on the opposite shores.

Suppose two of us are known to have been together on Broadway, but now one of us is in eastern Connecticut and the other at the eastern end of Long Island. One theory might be that we traveled together to the eastern end of Connecticut and then, while one of us stayed there, the other crossed the Sound in some way or other, even though we could not swim that far, there was no regular boat service, and the only evidence of a bridge having been built and then destroyed is that one of us is in eastern Connecticut and the other in eastern Long Island. It would seem to me more probable that we parted company in Manhattan and, while one of us crossed by a known bridge to Long Island and then had good going along the southern shore of the Sound, the other crossed known bridges and travelled through Connecticut along the northern shore of the Sound. This seems to be the way the respective theories concerning the biogeographical relationships of South America, Africa and Australia stand except that we have some other facts. To continue the comparison: although there may be no direct evidence as how one of us came to be in eastern Connecticut and the other at the eastern end of Long Island, yet it is known that other people have left New York and gotten to these two places without crossing the eastern end of the Sound and, furthermore (to make the comparison more accurate), we must put in as a part of the argument that no one was ever actually known to cross directly from eastern Connecticut to Long Island or *vice versa.* In the face of such evidence he would be rash indeed who would hold to the first theory as to our movements after we left Broadway.

Now I know very little about geology and still less about fossil mammals, but I am willing to take on faith the conclusions of well-accredited students of these subjects if the conclusions seem to have been reached by logical deduction from reasonable premises and if the assertions of fact are not too widely different from my recollection of the assertions of fact made by students who have reached other conclusions from what seem to me to be unreasonable premises. It would be out of place here to give the details of Matthew's analysis of vertebrate, especially mammalian, paleontology. He takes up group after group and outlines their fossil record showing that they

> accord fully and in detail with the principles[5] here set forth, and to be impossible of explanation except upon the theory of permanence of the ocean basins during the Cenozoic era. While the prominence of the Holarctic region as a center of dispersal is ascribed to its central position and the greater area, some evidence is given to show that climate is also a factor in the greater progressiveness of the northern, since it is also noticeable in the southern as compared with tropical faunæ.
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> The distribution of the Reptilia appears to be in conformity with the principles here outlined, and extends their application to the Mesozoic era. The distribution of birds and fishes and of invertebrates and plants is probably in accord with the same general principles, modified by differences in methods of dispersal. The opposing conclusions that have been drawn from the distribution of these groups are believed to be due to an incorrect interpretation of the evidence. A few instances, which have been prominently used to support opposing conclusions, are analyzed and shown to conform to the conclusions above set forth, if interpreted upon similar lines as the data for mammalian distribution.

As an example of the widely divergent conclusions which may be drawn from the same data concerning present-day distribution

[5] Permanency of the abyssal oceans; climatic cycles from extremes of cold or arid zonar climates culminating in glacial epochs, to the extremes of warm, humid, uniform climates, associated with cycles of moderate elevation and submergence, respectively, of continents; the cyclic development of progressive groups of animals in the great northern land mass and their dispersal southward as the result of these climatic changes.

I take the liberty of referring to my paper on the spiders of the Greater Antilles.[6] On pages 139 and 140 it is shown that sixteen Antillean genera, selected in a rather random fashion, are found to-day in regions connected by a certain hypothetical system of trans-oceanic bridges and not elsewhere. In some cases there appears to be almost no specific difference, even, between spiders whose present range is far from continuous. In fact, this set of data and other instances mentioned in that paper seem to me to furnish as strong evidence for such bridges as is given by the recent distribution of any one group of organisms, and yet I felt that this was not at all the explanation. It seemed more reasonable to believe that spiders had dispersed by the way of Holarctica on land masses which were practically the same as they are now and that the present discontinuous distribution of the ancient types is brought about by the fact that they are merely relicts which are now found far separated from each other.

Entomologists will at once think of a number of species which have reached the United States in historic times from Mexico and many will use these in a contention that much of our fauna has been derived from the south. I believe that the movement has been largely the other way and that the "southern element" of our fauna is largely made up of those things which have dropped behind in the general southern movement. As in any stream there are back eddies, so in the stream of dispersal we must expect back eddies (especially when man makes a channel as he did when he planted a large number of potatoes up to the former habitat of the Colorado potato beetle or grew great quantities of corn and other cereals for the chinch bug) but the eddies do not indicate the direction of the main stream. In their progress toward the equatorial region the streams of dispersal leave pools here and there—the stranded relicts of an ancient fauna. There are doubtless numerous swirls and back currents, while near their mouths these streams of dispersal may be much subject to "tides" due to minor, *i. e.*, measured by centuries, fluctuations of climate, but their general movement is, nevertheless, from the poles toward the equator. Since the northern polar regions have the larger land masses and better facilities for such dispersal-stream flow, the larger movements have been from the north, but simliar, though smaller, currents are to be expected in the southern hemisphere.

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[6] Lutz, F. E., 1915. "List of Greater Antillean Spiders with Notes on their Distribution." *Annals*, N. Y. Acad. Sciences, XXVI, pp. 71–148.